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ONTOGENY OF THE PRIMARY AXIS
OF SOJA MAX

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF BOTANY

1932

By
WILLIS H. BELL

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ONTOGENY OF THE PRIMARY AXIS OF SOJA MAX
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WILLIS H. BELL

(WITH THIRTY-SEVEN FIGURES)

Introduction

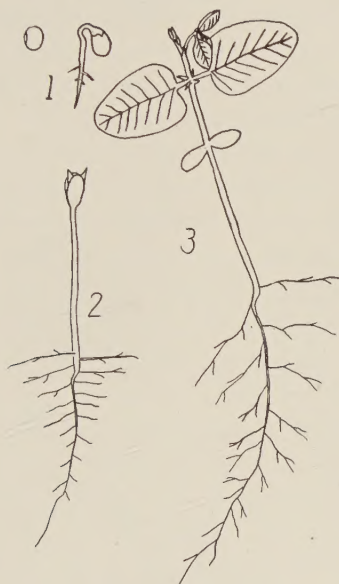
A voluminous literature dealing with nodule development and physiological relationships of the soy bean (*Soja max* Piper) has accumulated, but apparently the only strictly anatomical work has been a paper on the floral development by GUARD (4) and a brief seedling investigation by COMPTON (2). The present study has been undertaken to investigate the development of the primary axis. The variety used was the commercial Mammoth Yellow. PIPER and MORSE (6) have given the following description of this variety: "Plants stout, erect, bushy, maturing in about 145 days, pubescence gray; flowers white." At maturity the plants may be either bushy, with only a few internodes elongated, or vine-like, with more internodes elongated, depending upon physiological conditions of growth. The first leaves are simple and opposite and at right angles to the plane of the cotyledons. All other leaves are alternate and trifoliately compound. The flowers of this variety are in axillary racemes. The aerial portions of the plant are pubescent with simple hairs.

Investigation

The plants were grown under greenhouse conditions, and seedlings ranging from two to twenty days old were fixed for study. The stem and hypocotyl were fixed either in formal-acetic-alcohol or in chromo-acetic acid, and the root in chromo-acetic acid. The material was run up through alcohol and chloroform, imbedded in paraffin, sectioned at 12 μ , mounted serially, and stained with safranin and gentian violet. Drawings were made with the aid of a micro-projector and camera lucida.

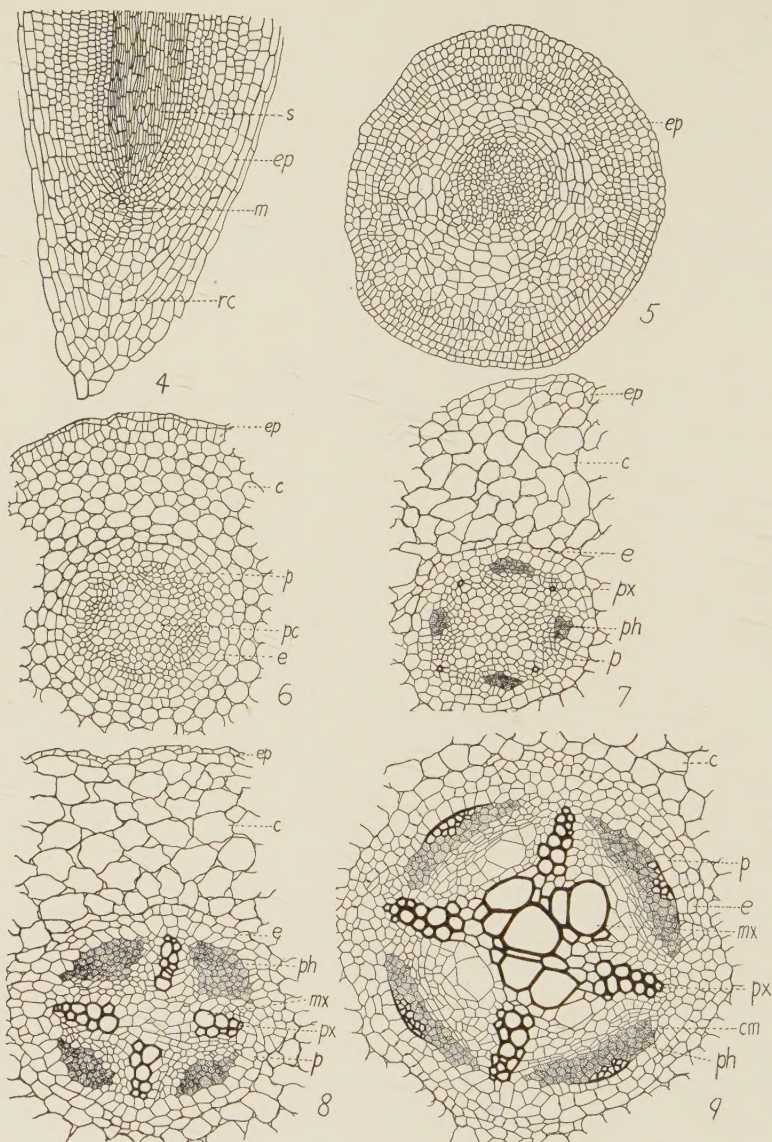
GERMINATION.—After imbibition of water the young primary root pushes through the seed coats and rapidly establishes itself as

an absorbing organ (fig. 1). The hypocotyl elongates, pulls the cotyledons up through the soil, and the seed coats are shed before the cotyledons appear at the surface of the ground (fig. 2). The cotyledons remain folded together as in *Phaseolus* until they are several centimeters above the surface of the soil. The epicotyl elongates but little until after the cotyledons unfold, and then it develops rapidly (fig. 3).



FIGS. 1-3.—Fig. 1, early stage in germination. Fig. 2, stage in germination after final elongation of hypocotyledonary arch. Fig. 3, young seedling with first true leaves fully developed.

PRIMARY ROOT.—The primary root at the completion of primary differentiation is a tetrarch radial protosteles (fig. 9). It is differentiated from a meristematic group of cells at the tip of the hypocotyl (fig. 4). Development is according to JANCZEWSKI'S (5) "fourth angiospermous type," in which the stele, cortex, epidermis, and root cap do not arise from definite histogens but from a common group of meristematic cells (fig. 4). The root cap is the first tissue differentiated, and consists of several layers of loosely packed parenchyma cells overlying the root tip. The epidermis is uniseriate and develops



FIGS. 4-9.—Fig. 4, longitudinal section of root tip (*s*, stele; *ep*, epidermis; *m*, meristem; *rc*, root cap). Fig. 5, cross-section of primary root above root cap showing epidermis differentiated. Fig. 6, same at time of differentiation of stele and cortex (*c*, cortex; *p*, pericycle; *e*, endodermis; *pc*, procambium). Fig. 7, same showing first protoxylem and protophloem (*ph*). Fig. 8, same showing primary xylem partially differentiated (*px*, protoxylem; *mx*, metaxylem; *ph*, primary phloem). Fig. 9, same after cambial activity has been initiated (*cm*, cambium).

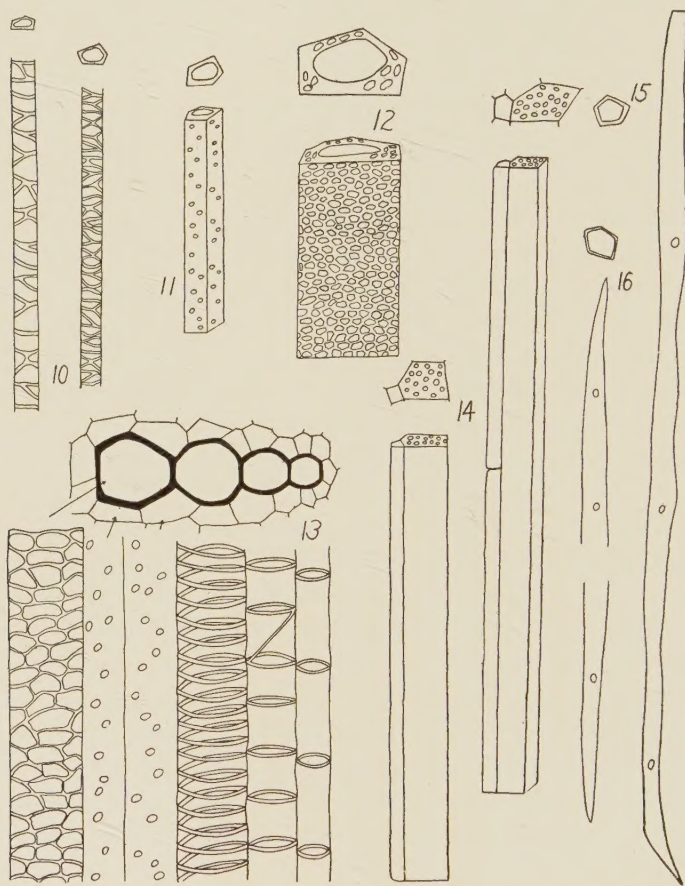
root hairs early in ontogeny (fig. 5). The cells of the cortex, except those of the endodermis, become large and loosely arranged with intercellular spaces while the cells of the stele are smaller and more compact (fig. 6). The primary xylem is exarch in its development, the first cells of the protoxylem differentiating from the procambium at four points adjacent to the pericycle (fig. 7). The one to three protoxylem vessels differentiated at each of the four points show spiral-reticulate markings on their walls (fig. 10). Metaxylem is matured progressively inward from the protoxylem points (fig. 8). The first metaxylem vessel segments have pitted walls with a single row of pits in each (fig. 11). The undifferentiated cells at the center of the primary root enlarge considerably and differentiate as metaxylem (fig. 9). The majority of these cells develop into short vessel segments with densely pitted walls (fig. 12). Some of the cells of this later developing metaxylem remain parenchymatous and ultimately differentiate into thick walled connective tissue.

The cells lying between the protoxylem points and adjacent to the pericycle differentiate centripetally as primary phloem (fig. 7). The first cells of the primary phloem remain parenchymatous and are crushed against the pericycle upon the initiation of cambial activity (fig. 9). The cells immediately beneath this parenchyma develop into phloem fibers. The remainder of the primary phloem consists of scattered parenchyma cells, sieve tubes, and companion cells. The sieve tube may be the same length as the companion cell or it may be equivalent in length to two companion cells (fig. 14). Cambial activity is initiated while the cells at the center of the root are still parenchymatous. At first activity is greatest immediately beneath the phloem, resulting in the crushing of the protophloem (fig. 9).

At about this time or somewhat earlier, the pericycle gives rise to secondary roots which dissolve their way through the cortex as they develop. The development of the primary body of the secondary root is identical with that of the primary root, except that ordinarily only one large metaxylem vessel instead of several is matured in the center of the root. The secondary root is usually smaller than the primary root, and may be diarch, triarch, or tetrarch.

HYPOCOTYL.—The hypocotyl as interpreted in this paper is that portion of the plant axis between the cotyledons and the true root.

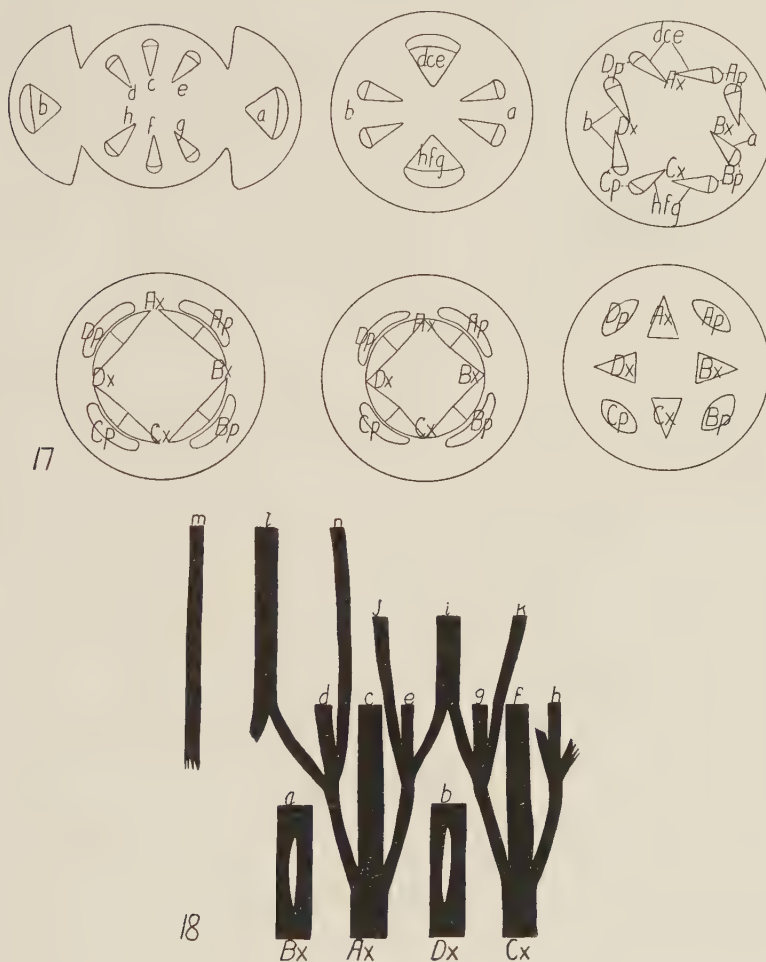
The lower portion of the hypocotyl is rootlike while the upper part is similar to the stem in the orientation of its tissues (figs. 19, 26). Upon germination the hypocotyl elongates as a result of meristematic



FIGS. 10-16.—Fig. 10, histology of protoxylem vessels of root. Fig. 11, histology of first metaxylem vessels differentiated in root. Fig. 12, histology of metaxylem vessel in center of root. Fig. 13, histology of primary xylem of stem. Fig. 14, sieve tubes and companion cells from root. Fig. 15, histology of phloem fibers of root. Fig. 16, immature pericyclic fiber from stem.

activity in the region of the hypocotyledonary arch (fig. 1). Procambial differentiation in the embryonic and elongating hypocotyl results in continuity of the procambium of the root and of the double

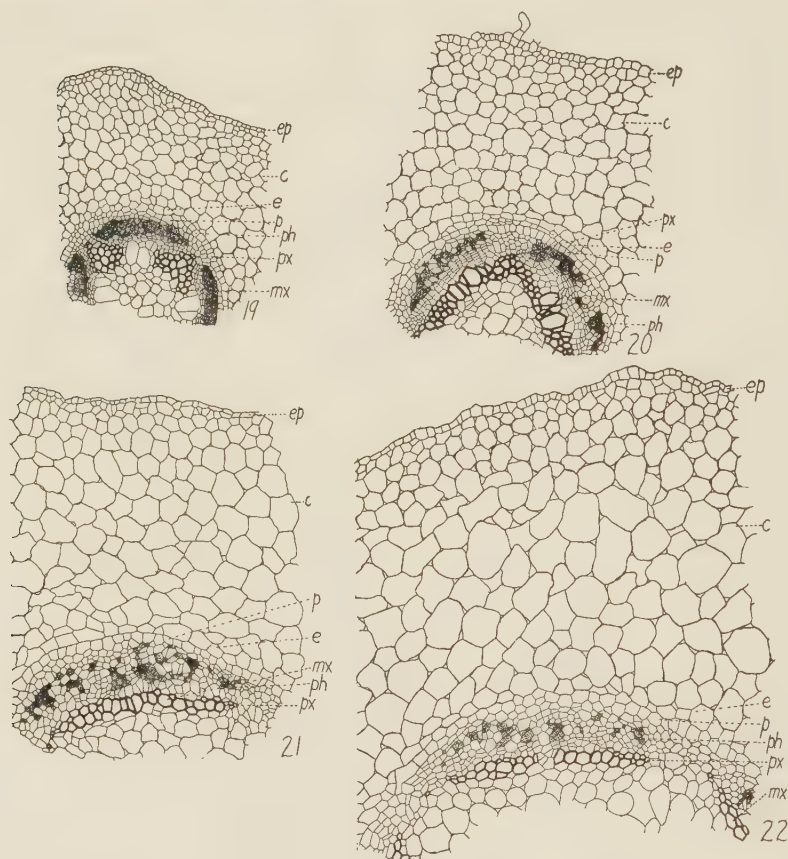
bundle to each cotyledon. Reorientation of the procambial strands in the lower part of the hypocotyledonary axis results in a transition



FIGS. 17, 18.—Fig. 17, diagrammatic cross-sections at different levels of the hypocotyl, illustrating method of root-stem transition and relationship of vascular supply of cotyledons and epicotyl to that of root. Fig. 18, diagram of main vascular supply of cotyledons and leaves at first three nodes.

between the radial protostelic structure below and the endarch collateral condition above. In this manner the four endarch collateral

bundles representing the traces to both cotyledons are differentiated against the tetrarch radial protosteles of the root (figs. 17-26).



FIGS. 19-22.—Fig. 19, cross-section of hypocotyl just above level of root showing xylem groups about to bifurcate. Fig. 20, same showing siphonostele as a result of xylem divergence in root-stem transition. Fig. 21, same showing xylem divergences in contact by their metaxylem. Fig. 22, same showing xylem divergences entirely separated by parenchyma.

The exact manner of reorientation of the hypocotyledonary vascular system is shown in figures 17 and 18. The double bundle *a* of one cotyledon passes downward as two groups, which upon undergoing transition just above the root tie against the xylem *bx* and one wing of the phloem *bp* and *ap* of the root. The double bundle *b* to the

other cotyledon is differentiated against xylem *dx* and one wing of the phloem *cp* and *dp* of the root.

COTYLEDONS.—The cotyledons are sessile and at maturity are fleshy and oval in shape (figs. 3, 29). The veins of the cotyledons are divergences from the double bundle entering at the base. After maturation of the opposite leaves the cotyledons are dropped from the plant.

EPICOTYL.—Prior to germination the epicotyl of the embryo has differentiated several foliage leaves. The first leaves, which are simple and opposite, are differentiated at right angles to the plane of the cotyledons. The leaf primordium arises as a conical crescentic divergence from the apical meristem, which because of meristematic activity broadens laterally at its base until the entire periphery of the growing point is involved. This lateral activity results in the differentiation of two stipules for each leaf. The leaf primordium elongates with the cells at its apex differentiating a blade and the cells at the base elongating to form the petiole (fig. 27).

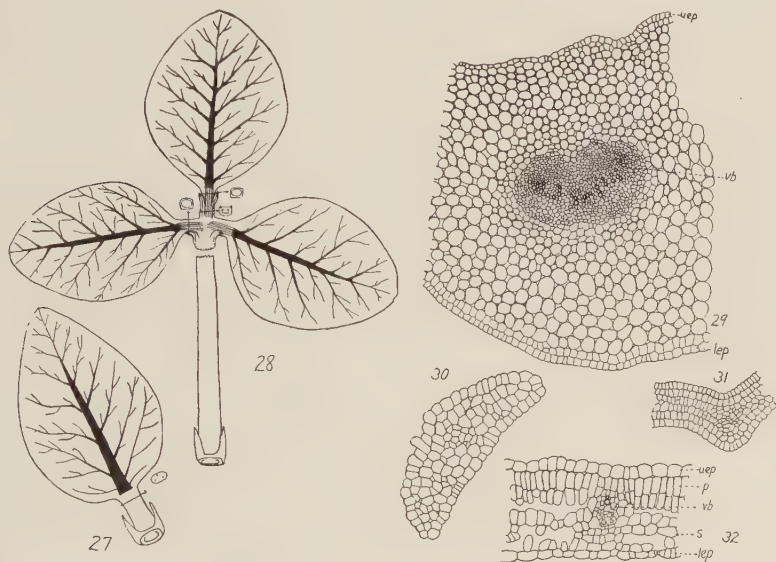
The primordia of the axillary flower buds are laid down at about the same time as are the associated leaf primordia. The procambial strands of the axillary bud are anastomosed with the downwardly differentiating strands of higher leaves at the node immediately below the point of divergence of the axillary bud.

In the development of the vascular system of the leaf the lateral bundles to the stipules converge with the median bundle at the base of the petiole. Meristematic activity continues in each stipule, resulting in the differentiation of a mesophyll. The veins to the stipule are divergences from the lateral bundle. Above the point of convergence of the median and lateral bundles the vascular system of the petiole appears stemlike, with several bundles in annular arrangement. Near the base of the lamina these bundles converge again to form a crescentic vascular ring. The blade is differentiated from a group of meristematic cells at the apical end of the leaf primordium (fig. 30). At first meristematic activity is general throughout, resulting in six to eight layers of cells (fig. 31). Differential growth eventually develops a blade with a single palisade layer and typical spongy parenchyma (fig. 32). Stomata are present in both the upper and lower epidermis but are more abundant in the lower.



FIGS. 23-26.—Fig. 23, cross-section of hypocotyl through transitional level showing cambium differentiation. Fig. 24, same showing primary xylem and phloem of transitional stage broken up into groups prior to endarch collateral orientation. Fig. 25, same showing both endarch and transitional xylem. Fig. 26, same after endarch collateral situation has been entirely attained.

The procambial strands which ultimately form the vascular skeleton of the blade are outward extensions of the median and lateral bundles of the petiole. In the leaf primordium the median bundle matures first, with the lateral bundles differentiating and maturing slightly later. The downward extensions of both are progressively matured as the hypocotyl and first internode elongate.



FIGS. 27-32.—Fig. 27, habit sketch of simple leaf. Fig. 28, same of compound leaf. Fig. 29, cross-section of a cotyledon (*uep*, upper epidermis; *vb*, median bundle; *lep*, lower epidermis). Fig. 30, cross-section of embryonic leaf. Fig. 31, cross-section of partially developed leaf prior to maturation of tissues. Fig. 32, cross-section of mature leaf (*p*, palisade parenchyma; *vb*, vascular bundle; *s*, spongy parenchyma).

One compound leaf is differentiated at right angles to the plane of the first pair of opposite simple leaves early in ontogeny (fig. 28). The development of this leaf is similar to that of the first true leaves just described. The median and lateral bundles of the trace are differentiated against the lateral bundles to the first leaves just above the cotyledonary plate. The stipules and petiole mature as just described but the petiole of the compound leaf undergoes much greater elongation. Instead of one meristematic group of cells at the tip of the primordium developing a blade, three regions of activity appear, giving rise to a trifoliate compound leaf, each leaflet receiving ap-

proximately one-third of the vascular supply of the petiole. Two small secondary stipules are developed as lateral divergences at the base of the terminal leaflet, and another pair immediately below the divergence of the two lateral leaflets (fig. 28). One small endarch bundle extends downward from each of these stipules and converges with the endarch groups to the leaflets which form the median and lateral bundles at the base of the petiole.

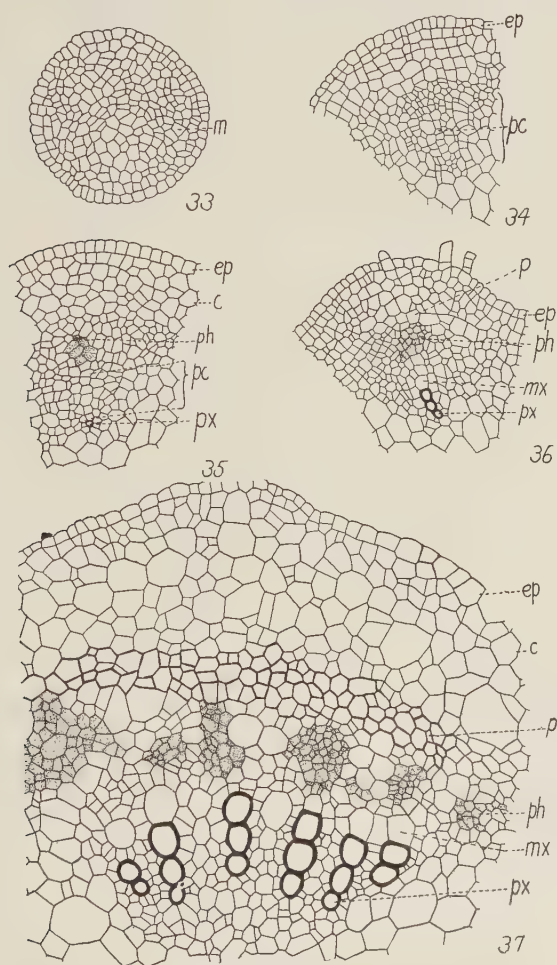
As seen in embryo, the median bundle *c* and the lateral bundles *d* and *e* of the trace to one of the opposite simple leaves pass downward and converge against the xylem *ax* and one wing of the phloem *ap* and *dp* of the root (figs. 17, 18). The trace *fgh* to the other opposite leaf converges with the xylem *cx* and one wing of the phloem *cp* and *bp* of the root. The trace *ijk* of the first alternate leaf is differentiated against the lateral bundles *e* and *g* of the opposite leaves at a level just above the cotyledonary plate (fig. 18). The trace *lmn* of the second alternate leaf converges against the lateral bundles *d* and *h* of the opposite leaves.

STEM.—The mature primary body consists of an endarch collateral dictyostele, pericycle, cortex, and epidermis (fig. 37). The pericyclic cells immediately external to the vascular bundles differentiate as fibers but in the region of the medullary rays remain parenchymatous. The primary vascular skeleton of the stem is a dictyostele consisting of the common bundles of the leaf traces.

The procambial strands may be recognized early by the greater density of the protoplasmic contents of their cells (fig. 34). The procambium adjacent to the undifferentiated parenchyma in the center of the stem matures as protoxylem (fig. 35). There are usually three strands of protoxylem (figs. 36, 37). The first strand shows widely separated annular markings (fig. 13) and is normally not collapsed at the time of maturity of the primary body. The later differentiated protoxylem strands show closer annular and spiral markings, the last formed consisting of tight spirals. Usually all the vessel segments have the histology of protoxylem but a few metaxylem vessels with pitted walls may develop. A large part of the primary xylem is parenchymatous at first and later matures as connective tissue.

Primary phloem is differentiated from the procambium in contact

with the pericycle and directly external to the primary xylem (figs. 35-37). The primary phloem consists of groups of sieve tubes and companion cells separated from each other by parenchyma (fig. 37).



FIGS. 33-37.—Fig. 33, cross-section through meristem (*m*) of epicotyl. Fig. 34, portion of stem showing differentiation of procambium. Fig. 35, cross-section of stem through region of vascular bundle at time of protoxylem differentiation. Fig. 36, same through vascular bundle. Fig. 37, same through median bundle to leaf.

The relationship between the sieve tubes and companion cells is similar to that in the root (fig. 14).

Summary

1. The root of the soy bean is developed according to JANCZEWSKI'S "fourth angiospermous type," and at maturity is a tetrarch radial protostele which, as COMPTON (2) and DE CANDOLLE (1) point out, is common to many Leguminosae and especially to the Phaseoleae of which the soy bean is a member. A conical mass of parenchymatous cells comprises the root cap. The epidermis consists of a single layer of cells from which root hairs arise. The cortex is composed of several layers of parenchymatous cells and the endodermis and pericycle are each a single layer. Secondary roots arise from the pericycle. The anatomy of the secondary root is similar to that of the primary root except that usually only one large metaxylem vessel is matured in the center of the root instead of several. The protoxylem of the primary root consists of one to three spiral-reticulate vessels. The metaxylem matures in two stages and differentiates as pitted vessels and parenchyma. Part of the primary phloem is crushed at the initiation of cambial activity while the remainder differentiates as fibers and groups of sieve tubes and companion cells interspersed with parenchyma. A sieve tube may be the same length as the companion cell or may equal two companion cells in length.

2. Root-stem transition in the Phaseoleae is either low or intermediate, being low in the soy bean. As they pass upward the four exarch radial vascular groups of the root bifurcate and reorient as eight endarch collateral bundles.

3. The double traces of the cotyledons pass downward and converge against two vascular groups of the root in the same plane.

4. The cotyledons are fleshy photosynthetic leaves which drop off after maturation of the first pair of opposite leaves.

5. The first leaves are simple and opposite with a pair of stipules at the base of the petiole. The trace to each leaf is composed of three bundles which are differentiated downward against the vascular system of the root at the level of transition.

6. The later leaves are alternate and compound and their traces, consisting of three bundles, pass downward through two or more internodes before anastomosing with the lateral traces of other leaves.

7. The stem consists of an endarch collateral dictyostele, peri-

cycle, cortex, and epidermis. The primary vascular skeleton is a dictyostele consisting of the common bundles of the leaf traces. Usually all the vessel segments have the annular and spiral thickening of protoxylem but sometimes a few metaxylem vessels with pitted walls can be observed. A large part of the primary xylem remains parenchymatous and later matures as connective tissue. Primary phloem consists of sieve tubes and companion cells separated by parenchyma. They have the same histology as in the root. The pericycle immediately external to the vascular bundles differentiates as fibers but in the region of the medullary rays remains parenchymatous.

The writer takes pleasure in expressing his indebtedness to Dr. H. E. HAYWARD, who has given valuable suggestions and criticisms during the progress of this work.

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